Muscle function in avian flight: achieving power and control

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Abstract:

Flapping flight places strenuous requirements on the physiological performance of an animal. Bird flight muscles, particularly at smaller body sizes, generally contract at high frequencies and do substantial work in order to produce the aerodynamic power needed to support the animal's weight in the air and to overcome drag. This is in contrast to terrestrial locomotion, which offers mechanisms for minimizing energy losses associated with body movement combined with elastic energy savings to reduce the skeletal muscles' work requirements. Muscles also produce substantial power during swimming, but this is mainly to overcome body drag rather than to support the animal's weight. Here, I review the function and architecture of key flight muscles related to how these muscles contribute to producing the power required for flapping flight, how the muscles are recruited to control wing motion, and how they are used in maneuvering. An emergent property of the primary flight muscles, consistent with their need to produce considerable work by moving the wings through large excursions during each wing stroke, is that the pectoralis and supracoracoideus muscles shorten over a large fraction of their resting fiber length (33-42%). Both muscles are activated while being lengthened or undergoing nearly isometric force development, enhancing the work they perform during subsequent shortening. Two smaller muscles, the triceps and biceps, operate over a smaller range of contractile strains (12-23%), reflecting their role in controlling wing shape through elbow flexion and extension. Remarkably, pigeons adjust their wing stroke plane mainly via changes in whole-body pitch during take-off and landing, relative to level flight, allowing their wing muscles to operate with little change in activation timing, strain magnitude, and pattern.

Birds power flight primarily by large pectoralis muscles that depress the wings at the shoulder. The dominant role and large size of the pectoralis muscle, therefore, enables a critical assessment of how muscle function is tailored to meet the mechanical power requirements of flapping flight over a range of flight conditions. The smaller supracoracoideus muscle of birds, about one-fifth the size of the pectoralis, is the primary wing elevator active during upstroke, particularly at slow to moderate speeds and during hovering (at faster flight speeds, wing elevation is likely produced passively by aerodynamic forces acting on the wings, which remain extended during upstroke to maintain lift through bound circulation [1, 2]). Smaller extrinsic and intrinsic wing muscles assist in modulating wing orientation and controlling wing shape. These muscles likely contribute to adjustments of the wing's performance as an airfoil [3-7] and, thus, may indirectly affect flight power requirements. However, because of their small size the intrinsic muscles of the wing likely contribute little additional mechanical power for flight.

Prior analyses of muscle-tendon architecture have shown that muscles differ widely in their design for changing length while producing force, but due to their conservative properties for force production and relative fiber strain (ratio of activated length change relative to resting fiber length), skeletal muscles generally perform about the same amount of work in proportion to their mass [8-11]. Longer fibered muscles, such as the avian pectoralis, however are well suited to producing the larger movements required for moving the wings to produce effective aerodynamic power for weight support and to overcome drag. In addition to having longer fibers, greater operating strains also enhance the range of movement that a muscle generates. Thus, the operating strains of certain flight muscles are expected to be

greater than those of muscles that support an animal's weight during terrestrial locomotion [12] that contract over more limited strain ranges, allowing more economical force production. Muscles, having short fibers that attach to a longer tendon such as those found in the legs of terrestrial animals, produce large forces and can recover substantial elastic energy from their tendon and aponeurosis [12-15]. These muscles are best used for movements that require little net shortening or lengthening of the muscle. Consequently, pinnate muscles having these architectural features are commonly found in distal limb regions. The intrinsic wing muscles of birds are commonly short fibered and pinnate, and have long tendons. This enables these muscles to control distal movements of the wing while, at the same time, being small and light weight. Their function has not been much studied to date, beyond a few comparative functional anatomical descriptions [7, 16, 17] and assessment of their neuromuscular activity patterns [3, 16, 17]. Even so, these studies are important because they provide a framework for future studies that seek to assess how the smaller intrinsic wing muscles are used to achieve flight across different conditions, and in birds with differing wing designs and flight styles.

In the context of this earlier work, the functions of the two primary flight muscles of birds, the pectoralis and supracoracoideus, are reviewed here in relation to the mechanical power needed to meet the aerodynamic requirements for flapping flight. The vast majority of morphological and physiological work has largely focused on the pectoralis because of its dominant role in powering avian flight. Consequently, much of the review of avian muscle function will focus on the pectoralis, with particular comparison to its antagonist, the supracoracoideus. Preliminary in vivo analyses of the triceps and biceps muscles, which control wing shape via elbow extension and flexion, are also considered in relation to

changes in flight performance required for take-off, landing, and maneuvering flight. Future directions for research to improve our understanding of the neuromuscular control and functional design of avian flight are also identified.

Functional anatomy of primary avian flight muscles.

The pectoralis is a large muscle (~8-11% body mass; [15,16]) that attaches to the humerus of the wing at the deltopectoral crest (DPC; Fig. 1). Its main portion (sternobrachialis, SB) originates from an enlarged sternal keel, with more anterior fibers

[Figure 1 here]

arising from the furcula, or 'wishbone'. A much smaller portion (thoracobrachialis, TB) originates dorsally from ribs. The fibers of the thoracobrachialis and posterior region of the sternobrachialis insert on an internal aponeurosis that merges with the more anterior SB fibers before attaching to the DPC. In addition to producing mechanical work during downstroke, the pectoralis also pronates the wing. The smaller supracoracoideus lies deep to the pectoralis, also originating from the keel of the sternum and is about one-fifth of the pectoralis in mass (~2% body mass). By means of its tendon, which inserts and acts dorsally at the shoulder as a pulley, the supracoracoideus elevates and supinates the wing during upstroke [18-21]. Whereas the pectoralis is comprised of generally long fibers with modest pinnation (pigeon: 31 to 67 mm, mean 41 mm), the supracoracoideus is a classic bipinnate muscle with short fibers (pigeon: 15-21, mean 18 mm). It produces elevation and supination of the wing by means of a long tendon that passes dorsally over the shoulder, via the triosseal foramen of the avian pectoral girdle, before attaching to the dorsal surface of the proximal humerus adjacent to the DPC. The pectoralis is comprised mainly of fast-oxidative (Type

IIa) fibers (~85% in pigeons) with a smaller component of fast-glycolytic (Type IIb) fibers
118 [20, 21]. Fiber type composition of the supracoracoideus, to my knowledge, has not been examined in pigeons, but in the European starling is comprised of a greater fraction (68%) of
120 fast-glycolytic versus fast-oxidative fibers [22]; whereas, in zebra finches, Anna's hummingbirds [23], and Atlantic puffins [24], the supracoracoideus is exclusively comprised
122 of fast-oxidative fibers.

124 *In vivo assessment of avian muscle function during flight.*

Because of its focal insertion on the ventral surface of the DPC in pigeons (Fig. 1B),
126 doves, cockatiels, budgerigars, magpies, and certain other species of birds, forces produced by the pectoralis can be estimated directly by means of strains recorded using a strain gauge
128 bonded to the dorsal surface of the DPC (in several avian species the pectoralis also inserts along the ventral proximal shaft of the humerus, preventing this approach). Details for
130 exposing and attaching metal foil strain gauges to obtain strain-calibrated *in vivo* recordings of pectoralis force are described elsewhere [25, 26]. Although some uncertainty exists in the
132 calibration of DPC-strain to pectoralis muscle force [27], such recordings provide a reliable and temporally detailed recording of time-varying muscle force. Other methods for obtaining
134 muscle force and estimates of mechanical power output for bird flight also have their limitations [28, 29]. A similar skeletal-strain based approach to extract the time-varying
136 force transmitted by the supracoracoideus muscle via the muscle's tendinous insertion on to the proximal dorsal shaft of the humerus has also been used [30].

138 In combination with DPC strain-force recordings of the pectoralis and the supracoracoideus, *in vivo* measurements of muscle fascicle strain are obtained in localized

muscle sites by means of sonomicrometry, a technique based on measurements of the propagation of sound pulses within the muscle to determine length changes [31]. Because the sonomicrometry transducers lie adjacent to muscle fascicle bundles, they provide a measure of fascicle strain rather than muscle fiber strain *per se*. Nevertheless, the two measures are likely to be quite similar. In the large pectoralis, sonometric measurements obtained from multiple sites (anterior and posterior SB and TB) in pigeons showed similar fascicle strain levels in the larger SB portion of the muscle, but smaller strains in the most posterior SB and TB portions of the muscle [32]. By averaging the sonomicrometry data for fascicle strain across recording sites (weighted by the estimated fraction of muscle mass that each site represents) or by relying on a single recording site within the muscle and assuming the site is representative for the muscle as a whole, the total work of the muscle can be assessed based on the muscle's length change. Muscle work is therefore determined by averaging fascicle strain multiplied time fascicle length, in relation to the time-varying force the muscle produces. The product of muscle fascicle length change and force is visualized as a work loop over the course of a wingbeat, or muscle contraction, cycle (see Fig. 3). The timing of muscle activation is recorded simultaneously using fine-wire electromyography (EMG) electrodes inserted into and anchored adjacent to those fascicles for which a sonometric evaluation of strain is recorded [31]. The EMG provides a measure of the timing of muscle activation and relative motor recruitment in relation to muscle force and length change. In total, the force, strain and neuromuscular activation recorded from the muscle serve to describe the temporal dynamics of the muscle's contractile performance across a range of flight conditions.

Functional analysis of pectoralis and supracoracoideus muscles during flight.

The pectoralis muscle is activated to contract late in upstroke, prior to wing reversal (Figs. 2A). Force development follows soon after the start of activation (~ 2-8 ms in pigeons and cockatiels) and peaks early in the downstroke, continuing until the end

[Figure 2 here]

of downstroke. The pectoralis undergoes a slight stretch or remains nearly isometric (depending on the species and flight condition studied), as force develops late in upstroke and through wing reversal to begin the downstroke (Figs. 2 & 3). By developing force while nearly isometric or being briefly stretched, the rate of force rise and the magnitude of peak force are appreciably enhanced due to force-velocity effects [33, 34]. As a result, the work that the pectoralis performs is substantially increased while the muscle shortens during the remainder of downstroke. Deactivation of the pectoralis occurs early in the downstroke, almost coincident with the timing of peak force generation. This allows the muscle to relax to near zero force prior to being stretched passively in the upstroke. Importantly, this reduces the antagonistic ('negative') work required of the supracoracoideus to elevate the wing. The timing of pectoralis deactivation relative to its continuing force production points to the problematic nature of inferring muscle force production based on EMG recordings alone.

[Figure 3 here]

For those species studied [27, 35, 36], the in vivo force-length work behavior of the pectoralis is generally similar across a range of flight speeds and conditions (Fig. 3). As noted above, activation of the pectoralis in these species occurs late in upstroke, as the muscle is being lengthened (this is most extreme in the mallard, Fig. 3B) or is nearly

isometric, allowing the muscle to develop force rapidly for a given level of activation. In contrast to classical expectations for the operating fascicle strain of a muscle (~10-15% of resting length) based on isometric force-length properties [33, 34]), the pectoralis of these species undergoes strains of 32-40% during different flight conditions (take-off, ascending and descending flight, and changes in speed during level flight), stretching 20-30% beyond the muscle's resting length (measured when the wings are folded against the bird's body on the perch), and shortening 8-12% less than resting length. This large strain excursion underlies the ability of the pectoralis to perform substantial work during the downstroke of each contraction cycle. Forces produced by the pigeon pectoralis were found to vary about 40% across flight conditions, ranging from take-off and ascending flight to landing and descending flight [26]. Forces produced by the cockatiel pectoralis during level flight across speeds ranging from 1 to 14 m/s in a wind tunnel were found to vary 65% [35]. These forces are estimated to be less than 40-60% of the peak isometric force that the muscle can generate [26], reflecting in part the rapid shortening that the muscle undergoes to produce work. In cockatiels, doves and pigeons, the pectoralis achieves 58-73% of the maximum theoretical work output possible for the observed force and active strain range [30, 35] (Fig. 3A).

[Figure 4 here]

Not surprisingly, the supracoracoideus of pigeons exhibits mirror-like force, length and activation timing patterns relative to the pectoralis [30] (Fig. 4). As the main upstroke muscle, the supracoracoideus is activated late in downstroke just prior to wing reversal. The muscle develops force rapidly while being nearly isometric, reaching peak force very early in the upstroke. The early onset of force development by the

supracoracoideus likely reflects the its role in decelerating and re-accelerating the wing during the downstroke-upstroke transition, as well as its role in wing supination [19]. Estimates of the elastic energy storage within the supracoracoideus tendon (51±62 mJ during level and 88±85 mJ during ascending flight) are consistent with this role, given that the magnitude of inertial kinetic energy exceeds the amount of elastic energy stored and returned by the supracoracoideus tendon [30]. The additional inertial power of the wing's motion is likely transformed into useful aerodynamic power mainly in the downstroke, as has been traditionally assumed [37] . The rapid supination of the wing produced by the supracoracoideus is important for achieving a short duration upstroke, with the potential for positive lift generation in birds with wing-tip reversal flight kinematics [38] or for minimizing unwanted negative lift. It also maximizes the duration of downstroke lift production and was likely an important feature in the evolution of an active flapping flight stroke [19]. Rapid supination of the wing to initiate upstroke in rufous hummingbirds [39] is key to this species' ability to generate positive upstroke lift, which has been estimated to be 25-33% of their total lift production [40]. In pigeons, the amount of force produced antagonistically between the two muscles was estimated to be small [30]. During slow level flight, the negative work of the pigeon pectoralis just prior to the end of the upstroke is about 18% of the positive work the muscle performs during the downstroke. This may well reflect a role in absorbing inertial energy of the wing as it is decelerated late in upstroke [30]. By comparison, negative work of the pigeon supracoracoideus is 14% of the positive work that the muscle performs and occurs late in downstroke to decelerate the wing at this time.

The short fibers of the bipinnate supracoracoideus muscle require them to operate over large strains, similar to those of the pectoralis. Supracoracoideus fascicle strains range from 33 to 40% of the muscle's resting length during descending, ascending and level flight [30]. The supracoracoideus fascicles also undergo a smaller degree of stretch relative to their rest length (6 to 12% across flight conditions) compared with their net shortening strain (-27% for all flight conditions). This pattern of fascicle length change relative to resting length is opposite to the pattern of strain observed within pectoralis fascicles, which lengthen by 20 to 30% of their resting length before shortening to ~10% less than rest at the end of downstroke (Fig. 4). Interestingly, the modulation of muscle strain in the supracoracoideus reflects mainly differences in the degree of wing depression (stretching the supracoracoideus and its tendon) that occur at the end of downstroke across the three flight conditions that were studied. Because of its relatively small size, the pigeon supracoracoideus generates 1.6 times the mass-specific muscle power output of the pectoralis. This reflects the much greater operating stresses (force normalized to physiological cross-sectional area) of the supracoracoideus, which ranged from 85 to 125 kPa for descending versus ascending flight, compared with stresses of 50 to 58 kPa in the pectoralis across the same flight condition [30], and 57 to 76 kPa in an earlier study of the pigeon pectoralis when corrected for the muscle's estimated myofibrillar area [26].

Comparative data for avian pectoralis power output versus speed.

[Figure 5 here]

Because the pectoralis is the dominant avian flight muscle (in pigeons, the pectoralis represents 60% of total wing muscle mass, unpublished data), the muscle's power output can be used to assess how whole body power output and, indirectly, aerodynamic power output vary as a function of flight condition and speed in a bird. Measurements of pectoralis mechanical power output and wingbeat frequency have been published for black-billed magpies (*P. pica*), cockatiels (*N. hollandicus*), and ringed-neck doves (*S. risoria*) across a range of flight speeds while flying level and steady in a wind tunnel [27, 41] (Fig. 5). Except for magpies, the other two species showed a U-shaped power versus flight speed curve, generally consistent with aerodynamic theory. This reflects high induced power costs at slow flight speeds and hovering that decease as speed increases, and high profile and parasite power costs (due to increasing wing and body drag) at higher flight speeds. The absence of an observed increase in pectoralis muscle power at higher flight speeds in magpies may reflect either an inability of this species, with its lower aspect ratio and less pointed wings, to achieve sufficient thrust in order to overcome the profile and parasite drag costs it incurs at higher flight speeds limiting the top speed that it can achieve [27], or that the birds were unwilling to fly at faster speeds in the wind tunnel. Although the wind tunnel used to study the magpies was smaller (50% less in cross-dimensions of the working section) than that used to study the cockatiels and doves, artifacts such as a possible ground or wall effect [42] were not judged by the authors to be the basis for the magpies' lower power cost at faster flight speeds. In the two other species (cockatiels and doves), pectoralis muscle power output

at the fastest flight speeds exceeded that produced when the birds were nearly hovering (Fig. 5). Thus, although pectoralis power output was high as expected during 1 m/s flight in the magpies, it remains unclear why the muscle's power output did not reach or exceed this level at faster flight speeds.

Given that other muscles are involved in flapping flight and do mechanical work, it is certainly the case that the total muscle mechanical power requirement for flight is greater than estimates based on the pectoralis alone. In the study of pigeons, for which pectoralis and supracoracoideus muscle power output were both determined [30], inclusion of supracoracoideus power output increases the total power output of flight by nearly 25%. Pectoralis power output across flight modes was 3.2 times greater than that of the supracoracoideus but less than the nearly 5-fold difference in muscle mass. Together, these two muscles represent 71% (unpublished data) of the total fight muscle mass of a pigeon. If the remaining smaller extrinsic and intrinsic wing muscles perform the same relative mass-specific work, this would suggest a total power requirement that may be nearly 40% greater than that determined for the pectoralis alone.

Aerodynamic models for estimating the power requirements of the flight of birds at different speeds [43-45] are commonly used to infer ecological strategies for maximizing a bird's flight range or minimizing the metabolic power requirement for flight as a function of time [46]. Although measurements of pectoralis muscle mechanical power output are consistent with the general change in power versus flight speed (being highest at slow and fast speeds, with a minimum at an intermediate flight speed), the absolute magnitude of the power cost for flapping flight across species and speeds remains uncertain. Arguments for one approach and/or method being superior to

another remain unconvincing. This is due to assumptions and simplifications that quasi-steady aerodynamic theory makes to estimate flight power requirements, and uncertainties in the calibration of pectoralis force and assessment of regional fascicle strain profiles from localized fascicle recordings on the experimental side. More recent attempts to estimate muscle power output based on isolated work loop muscle measurements in relation to EMG recordings made during flight [28, 29] also have their limitations. These include estimating muscle recruitment from relative EMG magnitude across flight speeds to adjust the maximally stimulated muscle power measurements derived from *in vitro* work experiments. Such an approach necessarily determines the change in flight power requirements based on changes in recorded EMG intensity. It also results in lower estimates of flight muscle power requirements of cockatiels (minimum power cost = ~40 W/kg at 7 m/s) compared with those (74-79 W/kg at 5-7 m/s) obtained using DPC-based force measurements [27, 35]. Additional studies that refine the use of these approaches, or use other methods [47], will improve our ability to quantify the absolute power costs of flapping flight for particular species operating across various flight conditions. Consistent with the in vitro muscle work and EMG intensity results that ascribe change in muscle power output across flight speed due to changes in EMG intensity [28, 29], results based on in vivo fascicle strain, EMG, and DPC-strain calibrated force recordings [27, 35] also showed EMG intensity to be highly correlated with muscle force (R^2=0.92). In the latter studies, changes in EMG intensity accounted for 65% of the modulation of muscle power, with changes in fascicle strain amplitude accounting for 25% and changes in wingbeat frequency only 10% of the modulation in muscle power [27, 35].

Using measurements of DPC strain-calibrated pectoralis force and fascicle strain to determine *in vivo* pectoralis power output, the comparative power curves for the different species studied to date suggest that wing loading, as well as wing and tail shape, are likely important determinants of a species' relative muscle power cost. Doves have the highest wing loading (36 N/m^2) of the species studied to date [2] and correspondingly have the highest relative flight power cost over a broad range of speeds (Fig. 5). Magpies, have the lowest aspect ratio wings (5.0 versus budgerigars: 7.3, cockatiels: 7.0, and doves: 5.7) and rounded wingtips, which likely helps to lower their muscle mass-specific power requirements but may also limit the fastest speeds they can achieve.

At present, it would be imprudent to place heavy reliance on the accuracy of experimental or theoretical modeling results to specify precisely whether a species has a minimum power cost at a particular flight speed, given the uncertainty and limitations to the resolution and accuracy of currently available approaches used to estimate flight power costs. For example, whereas oxygen consumption data for cockatiels [48, 49] indicate a minimum metabolic power cost at 10 m/s, measurements of pectoralis muscle power data suggest a minimum in the range of 5 to 7 m/s [27, 29]. Combining the metabolic power results for cockatiels with their mechanical muscle power results [49] indicates that muscle efficiency increases with flight speed, ranging from 6.9 to 11.2% based on the muscle power data of Morris and Askew [29], or from 12.2 to 28.3% based on the DPC-pectoralis force and fascicle strain recordings of Tobalske at al. [27].

Differences in muscle efficiency are likely given that the shortening velocity of the pectoralis muscle fascicles varies with flight speed. For cockatiels [27, 35], fascicle shortening velocities ranged from 5.19 to 6.73 muscle lengths/s across flight speeds from

1 to 13 m/s. The range of efficiencies derived from in vitro muscle measurements adjusted for EMG intensity [29] are low compared with those expected for vertebrate skeletal muscle, which range from 20-28% at optimal shortening velocities [50]. It seems surprising that the evolution of flight muscle function in cockatiels and other birds would be constrained to substantially lower efficiencies. Although wingbeat frequency varies only slightly across flight speeds (10% in cockatiels), the magnitude of pectoralis fascicle strain changes in a shallow U-shaped pattern, paralleling changes in pectoralis force [29], which results in the overall muscle power versus speed relationship that is observed for cockatiels (Fig. 5). Although fascicle strain rate varies with flight speed, the generally uniform contractile properties of the pectoralis across a range of flight speeds [27, 29] (Fig. 3) reflect the strikingly uniform fiber type characteristics of the avian pectoralis [21-23]. This is in contrast to the much larger change in fascicle shortening velocity with running speed that occurs in the leg muscles of terrestrial animals [51-54].

Muscle function in relation to the control of take-off, landing and maneuvering flight.

Whereas the pectoralis and supracoracoideus are mainly responsible for producing the mechanical power required for sustained flapping flight in birds, it is unclear whether the activity of these large flight muscles is modulated to achieve maneuvering flight behaviors, or whether the smaller wing extrinsic and intrinsic muscles are recruited to adjust wing orientation and wing shape. Past work based on 3D kinematics, muscle force, and EMG recordings suggest two possibilities. In pigeons [6, 55] left and right pectoralis muscles appear to exhibit differential timing of force

development and magnitude, with downstroke of the outside wing phase advanced relative to the inside wing of a turn. In rose-breasted galahs [5], little difference in the kinematic timing of downstroke or pectoralis EMG activity was noted during 90^{o} turns. Instead, there was evidence of differential activation of the left and right biceps muscles, with the inside biceps showing stronger activity, indicative of increased elbow flexion and reduction of inside wing span. In both sets of studies, however, more detailed kinematics of wing shape and motion during these maneuvers was not available given the limited resolution of the motion-analysis systems used at the time. Future work will benefit from improved kinematic resolution during turning flight, combined with further study of left wing versus right wing muscle contractile asymmetry.

[insert Figure 6 here]

In studies of pigeons taking-off from an elevated perch platform, flying level and landing on a similar perch, measurements of wing, body and tail kinematics reveal little change in wing or tail movements relative to the bird's body [56]. Instead, most of the change in global orientations of the tail, wing and wing stroke plane, which determine the aerodynamic properties of the bird's flight stroke, are achieved by changes in body pitch (Fig. 6A). During take-off, pigeons pitch forward (head down) inclining their stroke plane to a more vertical orientation to provide increased thrust for acceleration after the take-off jump from the perch. During landing, the pigeon pitches back (head up), changing its stroke plane to a more horizontal orientation to help decelerate as it lands. Changes in global stroke plane angle during take-off and landing are significantly greater and less, respectively, than observed during level flight.

388 The uniform motion of the pigeon's wings relative to its body during take-off, level and landing flight, suggests that the control of wing and body movement across
390 these key phases of flight relies on subtle shifts in aerodynamic and inertial forces produced by the tail and wings relative to the body to control body pitch. The pitch
392 moment of inertia of a bird, though greater than its roll moment of inertia, is still quite small. As a result, slight shifts in the orientation of net aerodynamic force produce the
394 observed pitch acceleration. In pigeons, the shift in direction of net aerodynamic force need only be ~8 mm relative to its center of mass to produce the observed pitch moment
396 [56]. Consistent with this, no significant differences were observed in the neuromuscular activation (EMG) or contractile strain behavior of the wing muscles examined (Fig. 6B)
398 [57]. This result suggests that the control of body orientation and wing motion relative to the body does not require substantial changes in flight muscle activation and contractile
400 function. Instead, the highly maneuverable bodies of many birds (low pitch, roll and yaw moments of inertia) enables them to achieve changes in body and wing orientation that
402 allow rapid sharp turning, or to shift from take-off to landing flight, with subtle changes in neuromuscular function that are likely to prove challenging to identify.

404

Discussion and Summary.

406 Muscle function in bird flight depends on the production of substantial mechanical work performed at a high rate. Although skeletal muscles generally have a
408 similar capacity for generating mass-specific work, the avian pectoralis is well suited to performing work with large length excursions. This is a prerequisite for powering flight
410 because the wings must move through a large excursion during downstroke to produce

effective aerodynamic lift. The pectoralis achieves this by having relatively long
412 fascicles that shorten over a large fraction (up to 42%) of their length. The timing of muscle activation late in upstroke also allows the pectoralis to rapidly develop force
414 under nearly isometric or stretching conditions. This elevates the work that the muscle performs as it shortens (Fig. 3).

416 Because of its large size and principal role in producing aerodynamic lift, the contractile function of the avian pectoralis provides a valuable index for the power
418 requirements of flight based on measurements of its force production, contractile strain and neuromuscular activation. This is in contrast to the multiple muscle groups in the
420 limbs of running animals that contribute to muscle power for movement. Nevertheless, a functional examination of the broader suite of wing muscles is needed in order to
422 understand how flight movements, particularly those during maneuvering, are controlled. Although much smaller wing muscles may not contribute significantly to the mechanical
424 power underlying flight, by adjusting the orientation and shape of the wing they can alter the wing's aerodynamic properties and, thus, influence how aerodynamic forces and
426 power are shifted between the wings for maneuvering.

An unexpected result is that shifts in body, tail and wing movement during take-
428 off, level and landing flight of pigeons are achieved mainly by changes in whole body pitch, rather than by changes in wing or tail motion relative to the body itself. The degree
430 to which turning flight is achieved by left versus right asymmetries of smaller wing muscles, acting to 'steer' the bird around a turn, as opposed to modulation of the larger
432 power producing pectoralis and/or supracoracoideus muscles remains unclear. Evidence exists that both sets of muscles may contribute to the necessary aerodynamic asymmetries

that result in a turning maneuver. The low moments of inertia and highly maneuverable bodies of birds means that left versus right asymmetries in turning flight, or fore-aft asymmetries in aerodynamic force production during take-off and landing flight are likely to be small and challenging to identify.

Future studies will benefit from improved imaging that will allow detailed changes in wing shape, orientation and movement to be quantified and related to the timing and magnitude of muscle activation, and where possible, changes in muscle length, force and work. These measurements become increasingly difficult for smaller muscles, located more distally in the wing. Force measurements, in particular, are difficult to obtain for most muscles, hampering the ability to assess muscle force and work output in relation to maneuvering flight. In the case where muscles are too small, or forces cannot be recorded directly, in vitro or in situ measurements of muscle force [29] can play an important role for assessing the muscle's contractile properties and role(s) in flight. The remarkable ability of birds to fly over a range of speeds while often maneuvering through complex environments, makes understanding the neuromuscular and aerodynamic features of these flight behaviors of considerable interest to physiologists, biomechanists and aeronautical engineers.

Similarly, the aerodynamic and metabolic power requirements for flight are of considerable interest to avian and evolutionary ecologists interested in the strategies that birds use to forage and migrate to ensure a successful life history. For this reason, additional free flight data on bird metabolism, characteristic flight speeds and behavior need to be linked to additional experimental assessments of flight energy metabolism and musculoskeletal function. While quasi-static aerodynamic models can provide a rough

estimate of flight costs, the importance of non-steady aerodynamic effects on flight power costs are now well recognized and cannot be ignored. Thus, additional modeling and experimental studies that seek to yield improved measurements of muscle function and aerodynamic power output are needed.

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Figure Captions.

Figure 1. A) Anatomical organization of avian wing musculature (adapted from [3]), showing key muscles that have been studied, and B) showing the general sites used to record pectoralis force via deltopectoral crest (DPC) bone strain, pectoralis fascicle strain, and neuromuscular activation (EMG).

Figure 2. Representative *in vivo* recordings of pectoralis fascicle strain, neuromuscular activation (EMG), and force for three wingbeats in a cockatiel flying at 7 m/s in a wind tunnel. Adapted from [35].

Figure 3. Representative *in vivo* work loop patterns produced by the A) pectoralis of cockatiels (*N. hollandicus*) at three different flight speeds (adapted from [35]), and B) the pectoralis of three other species: ring-neck doves (*S. risoria*), pigeons (*C. livia*) and mallard ducks (*A. platyrynchos*) (adapted from [27, 31, 36]). The force produced by the muscle is plotted against its fascicle strain (L/L_o, where L_o is the muscle's resting length: strain = 1.0). In the first panel of (A) the dashed rectangle denotes the maximum work that the muscle could produce for its maximum force and strain; the realized work of the muscle is 68% of its theoretical maximum. The strain range for all muscles is the same (0.9 to 1.3, or 40% range of muscle length change), but force ranges differ in (B) due to the different sized muscles. The bold gray portion of each work-loop represents the period of neuromuscular activation measured by EMG. Arrows denote the direction of force and fascicle length changes.

Figure 4. Representative recordings of the pigeon supracoracoideus (wing elevation) fascicle strain, EMG and force, and pectoralis (wing depression) fascicle strain, EMG and

force recorded during takeoff from an elevated perch platform and level free flight at ~ 4.5 m/s (7 wingbeats are shown). Gray panels represent the downstroke for the initial four wingbeat cycles, with the upstroke in white background (adapted from [30]).

Figure. 5. Comparative flight power curves for three avian species, showing changes in pectoralis mass-specific muscle power (determined from calibrated DPC-strain force and fascicle strain recordings) versus flight speed in a wind tunnel (adapted from [27]).

Figure 6. A) Changes in wing stroke plane (SPA_{loc}) and body pitch angle (in global space) of a pigeon during successive wingbeats of take-off, mid-level flight, and landing (adapted from [56]). The strong correlation of wing stroke plane angle versus body angle is shown to the right. B) Representative in vivo recordings of muscle strain and activation (EMG) of extrinsic and intrinsic wing muscles of a pigeon during take-off, level (~ 4.5 m/s) and landing flight corresponding to a similar sequence shown in A) above (adapted from [57]).

running head: *Muscle function during avian flight*

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Figure 1 (Biewener)

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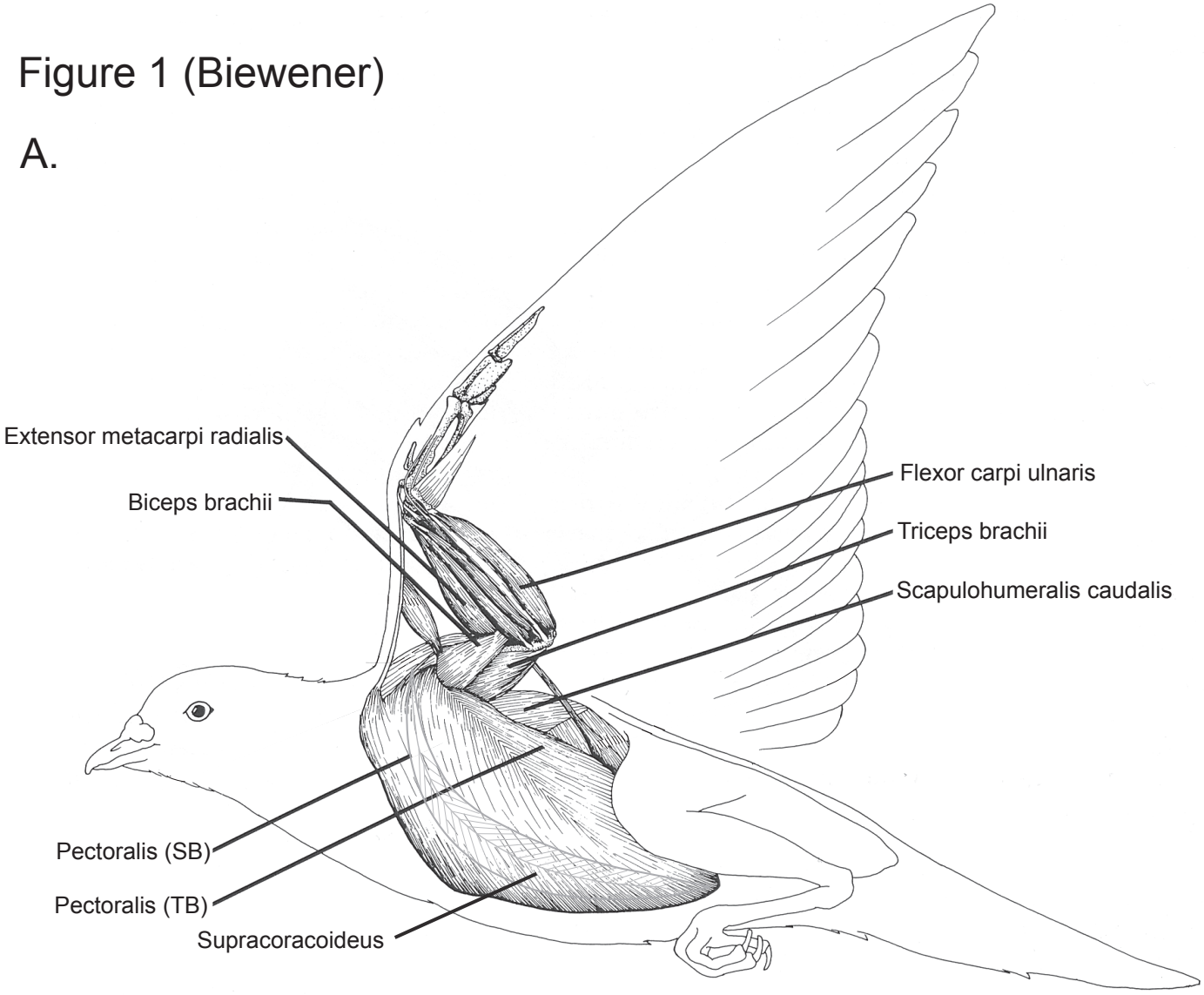

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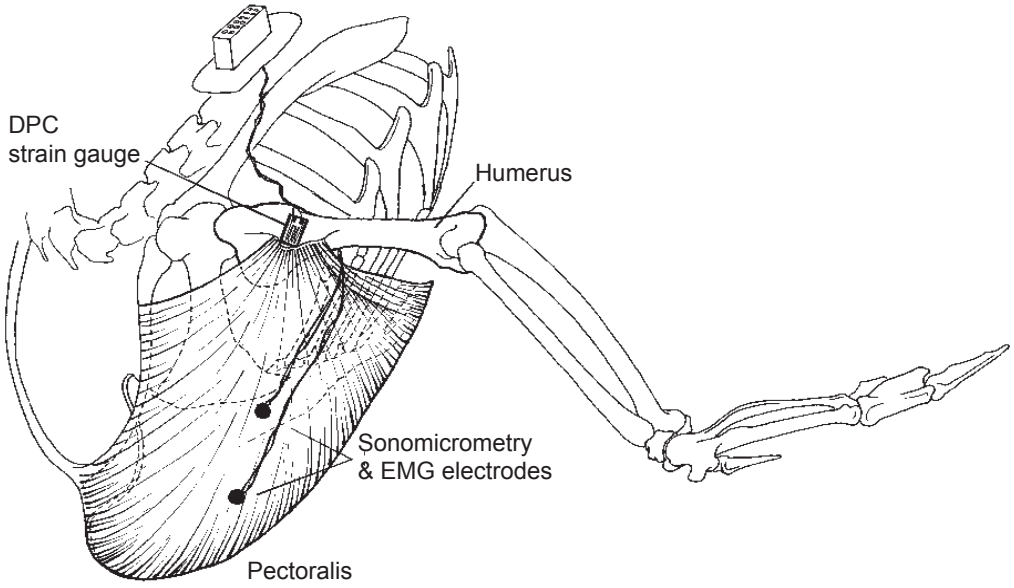

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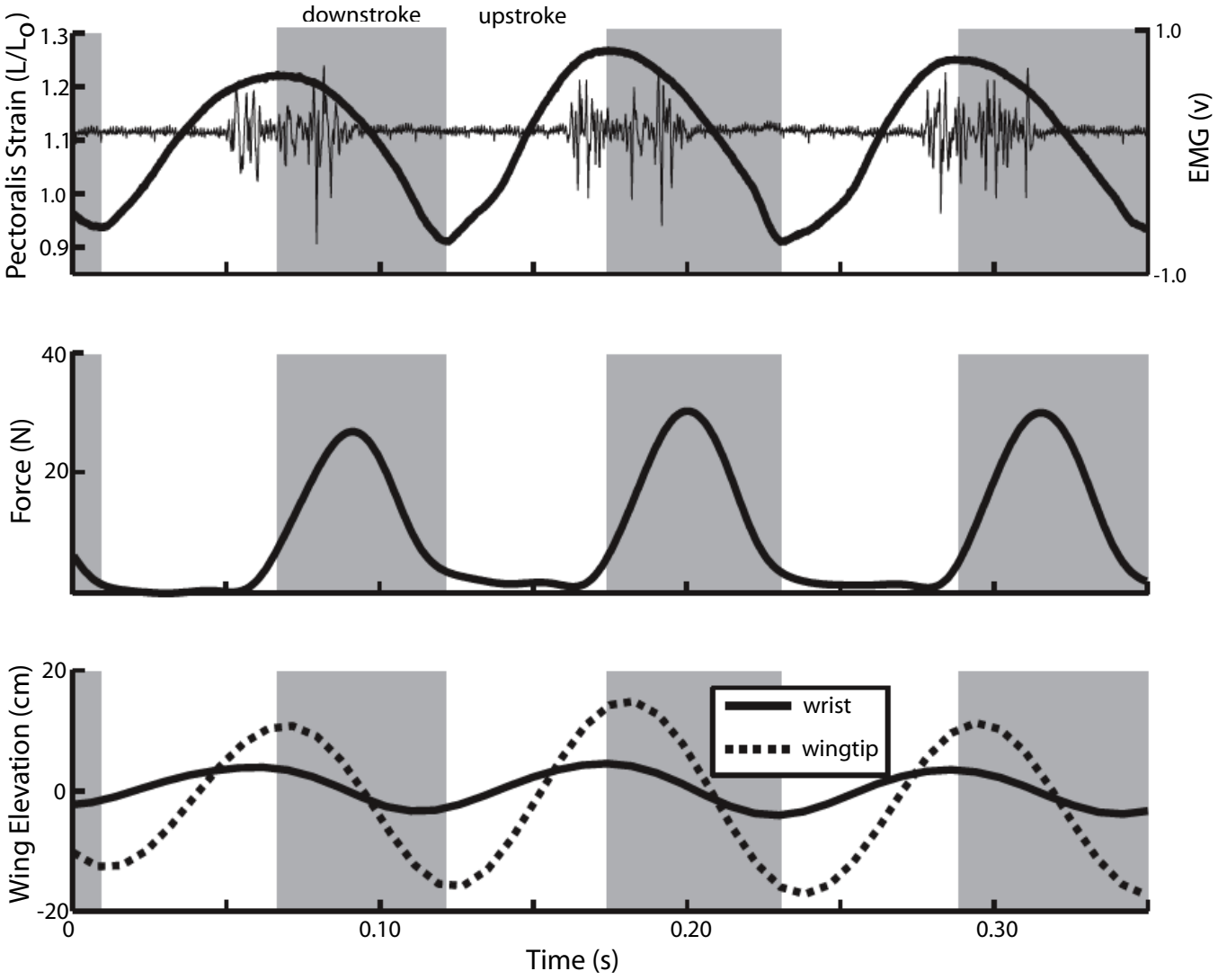

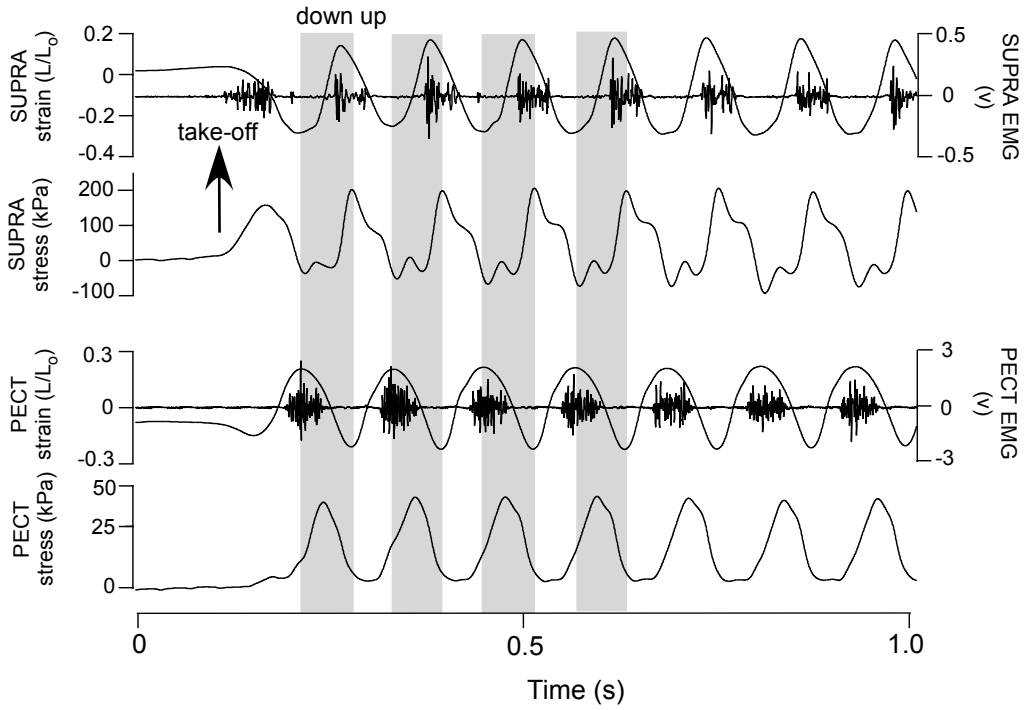

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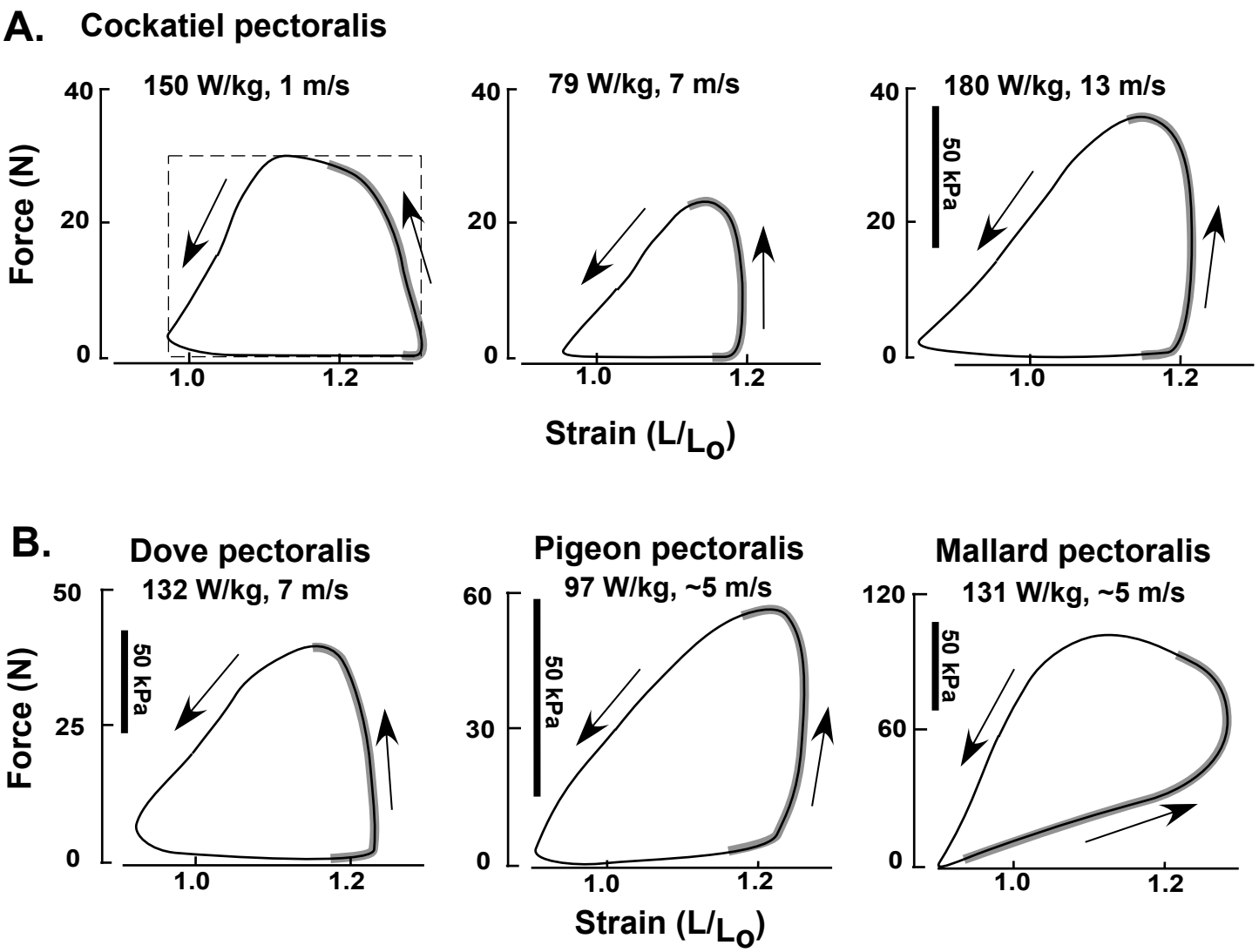
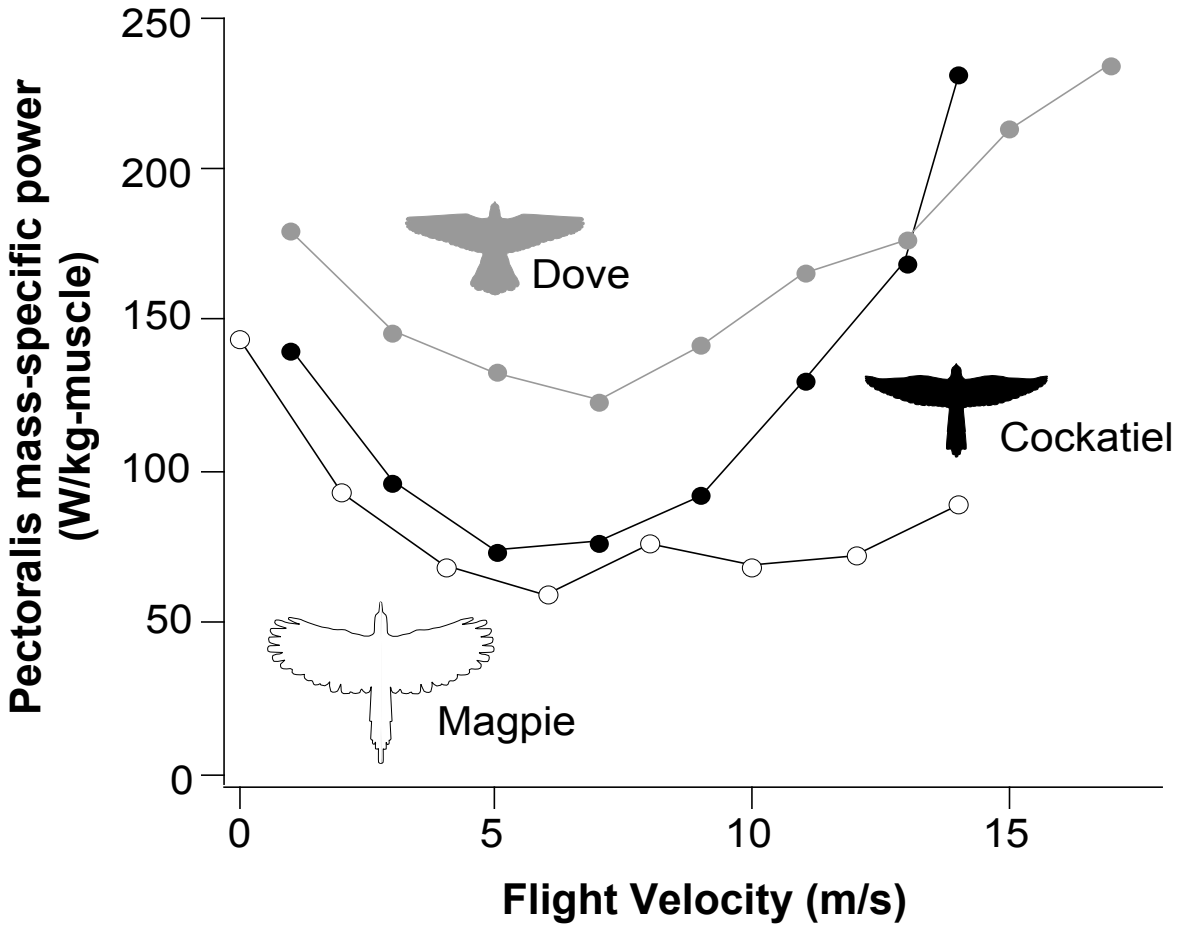


Figure 3 Biewener



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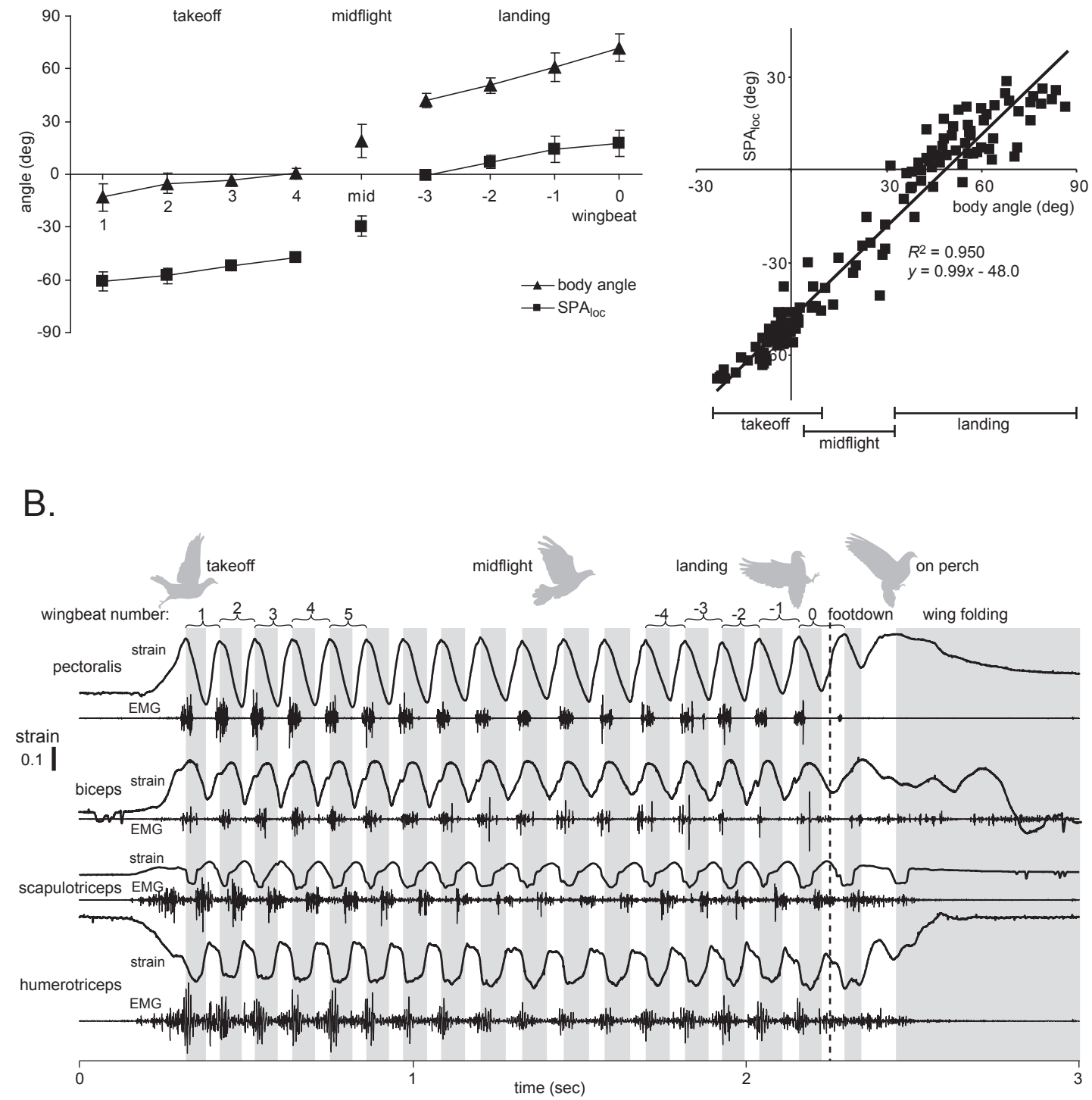

Figure 6. Biewener